An fMRI study of the selective activation of human extrastriate form vision areas by radial and concentric gratings

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The ventral form vision pathway of the primate brain comprises a sequence of areas that include V1, V2, V4 and the inferior temporal cortex (IT) [1]. Although contour extraction in the V1 area and responses to complex images, such as faces, in the IT have been studied extensively, much less is known about shape extraction at intermediate cortical levels such as V4. Here, we used functional magnetic resonance imaging (fMRI) to demonstrate that the human V4 is more strongly activated by concentric and radial patterns than by conventional sinusoidal gratings. This is consistent with global pooling of local V1 orientations to extract concentric and radial shape information in V4. Furthermore, concentric patterns were found to be effective in activating the fusiform face area. These findings support recent psychophysical [2,3] and physiological [4,5] data indicating that analysis of concentric and radial structure represents an important aspect of processing at intermediate levels of form vision.

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Results and discussion

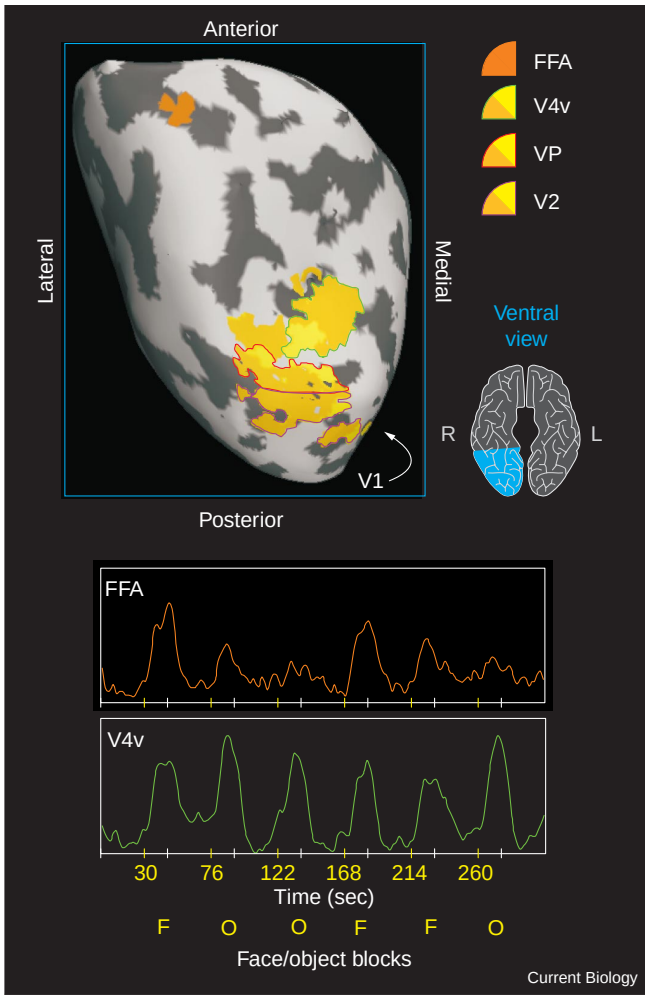
The present study was motivated by electrophysiological investigations of the response selectivity of macaque V4 neurons [4–6], and by recent human psychophysical findings from our laboratory [2,3] using random dot Glass patterns [7,8]. Gallant *et al.* [4,5] compared V4 responses to parallel sinusoidal gratings with responses to concentric, radial and hyperbolic gratings defined in polar coordinates. Although most V4 neurons responded to all of these stimulus classes, distinct subpopulations, totalling 16–17% of V4 cells, responded at least twice as strongly to either concentric, radial or hyperbolic stimuli than to any sinusoidal grating, whereas very few cells (0–8%) responded best to sinusoidal gratings [4,5]. As summarized by Gallant *et al.* [5], these polar stimuli have been proposed as an intermediate stage of form processing in several theoretical formulations and are also spatial analogues to the temporal pooling that underlies rotational and expansion/contraction flow-fields, suggesting an important parallel between form and motion analyses. Taking a very different approach, Kobatake and Tanaka [6] investigated the selectivity of V4 and IT neurons to a wide range of complex objects and then subtracted components to isolate the critical stimulus features. Of the 14 examples of critical features for V4 neurons (see their Figure 11), 9 have components incorporating circular or radial structure.

We have shown psychophysically that human vision is significantly more sensitive to concentric and radial structure than to parallel structure in Glass patterns [2,3]. Moreover, these experiments demonstrated that the sensitivity to concentric and radial organization resulted from spatially structured linear summation of orientation information. These findings suggested the existence of human neural populations tuned to concentric and radial organization such as those that Gallant *et al.* have found in the macaque V4 [4,5]. Here, we have used fMRI to determine whether such structured orientation pooling is an important feature of the human V4 area.

Data are presented for five subjects who were scanned in a 4.0 tesla, whole-body MRI system (Varian/Siemens). All subjects gave written informed consent, and the procedures were approved by the McGill University (Psychology) and the University of Western Ontario review boards for health sciences research involving human subjects. Details of the scanning and data analysis methodology may be found in the Supplementary material. In separate scan sequences within the same fMRI session, we mapped visual cortical retinotopy and also regions responding preferentially to faces and objects. We then examined the activation of regions of interest defined by these scans to the parallel and polar geometric patterns described below.

To delineate retinotopic maps, we used the phase-encoding procedure of Engel *et al.* [9]. Based on reversals of the field map, we were able to localize the upper field maps of V1, V2, V3(VP) and V4v in the inferior occipital lobe (see Figure 1). The objects/faces scan sequence, illustrated in Figure 1, consisted 16 second intervals of band-pass filtered, grey-scale faces and objects (F and O, respectively;

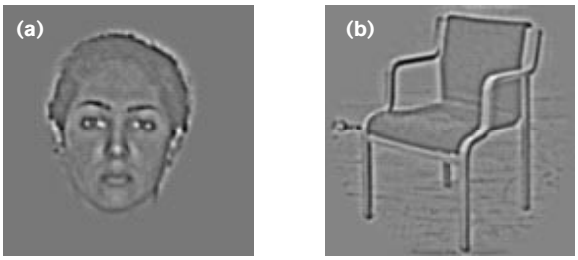
Figure 1



Functional imaging data were analyzed using Brain Voyager™ software. In the upper panel, regions of interest are displayed on an inflated ventral view of the posterior right hemisphere. Gyri are light grey, sulci are dark grey. The regions shown in color were taken from one representative participant. Retinotopic mapping is shown in alternating bright/dull yellow representing upper left quadrant areas abutting the vertical and horizontal meridians, respectively. This includes areas V2, ventral V3 (VP) and ventral V4 (V4v). Visual area V1 is not visible from this viewpoint. V4v, which was the focus of our study, is outlined in green, and the FFA is in orange. The lower panel illustrates the time course of the face/object scan. Patterned stimuli were presented for 16 sec intervals interspersed with 30 sec baseline intervals. The start of each face/object interval is indicated by a yellow tick mark on the horizontal axis and the end of each interval with a white tick mark. The class of stimulus (F/O) viewed during each period is indicated below the graphs.

Figure 2) interspersed with 30 second control fixation intervals in which a homogenous field of the same mean luminance (72 cd/m^2) was displayed. By subtracting object-specific activation from face-specific activation, a face-specific region was identified in the posterior fusiform gyrus, in the right hemisphere in all five subjects

Figure 2



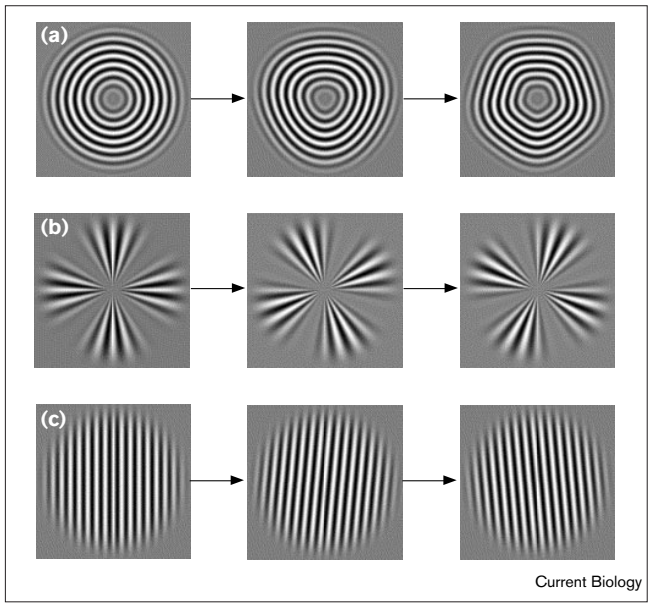
Examples of **(a)** face and **(b)** object stimuli used in face/object localization scan. Because of bandpass filtering, all stimuli were of the same mean luminance as the surrounding screen (72 cd/m^2). The spatial frequency spectra of these stimulus sets were closely matched (see Supplementary material).

(Figure 1). Because this area corresponds closely in location to the face-activated region described in posterior fusiform cortex by Kanwisher *et al.* [10], it will be referred to as the fusiform face area (FFA).

We then examined the activation of V1, V4 and FFA by the geometric patterns shown in Figure 3, presented in a separate scan sequence. The patterns consisted of concentric (C), radial (R) and parallel (P) gratings interspersed with mean luminance (L) fields in the sequence C-L-R-L-P-L-P-L-R-L-C with the same timing parameters as the F/O scan. This sequence was repeated three times with a rest period between each sequence. Subjects were instructed to fixate the center of the pattern, and to respond with a button press whenever a change in the pattern was noted. The average error rate was below 2% and did not differ across geometric patterns.

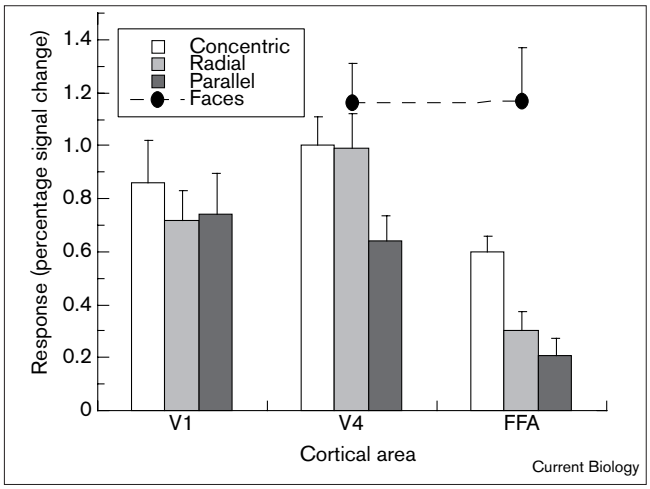
In all brain areas examined, the three geometric pattern groups produced strong activation relative to the mean luminance control condition ($F_{1,4} = 31.8$, $p < 0.005$). However, the relative strength of activation by concentric, radial and parallel gratings varied markedly across cortical regions (Figure 4), as indicated by the significant pattern by region interaction ($F_{2,8} = 10.4$, $p < 0.05$) in the overall analysis of variance (ANOVA) performed on these data. A summary of all the statistical comparisons made between stimuli may be found in Table 1. In V1, all three patterns produced comparable activation, indicating that we were successful in equating our three stimulus classes in terms of their effectiveness at this level. This is a necessary precondition for demonstrating differential effectiveness higher in the pathway. In V4, however, consistent with the configural orientation pooling hypothesis, parallel patterns provided significantly weaker activation than either concentric or radial patterns, which proved to be equally powerful stimuli for this region (Figure 4). Faces activated V4 at about the same level as concentric and radial patterns.

Figure 3



The concentric, radial and parallel geometric patterns used as stimuli in the main experiment. To maintain attention, **(a)** concentric patterns switched from perfectly circular to modulation by either a radial frequency of 3 or 5 cycles [16], **(b)** radial patterns rotated the contrast modulation of their arms by ± 22.5°, and **(c)** parallel patterns changed orientation by ± 6° every 2.5 ± 0.5 sec.

Figure 4



Responses (percentage signal change relative to baseline) in cortical areas V1, V4 and FFA. All three geometric pattern types produced statistically indistinguishable responses in V1. In V4, however, concentric (white) and radial (light grey) gratings produced significantly more activation than conventional parallel sinusoidal gratings (dark grey). Concentric patterns were significantly more effective stimuli than either radial or parallel patterns in FFA. For comparison, responses to faces (black circles) taken from a separate block of trials are shown. The error bars represent standard errors.

Previous fMRI data have shown that the human V4 generates stronger signals to relatively large chunks of a natural image than to a highly scrambled version of that image, whereas V1 responds equally to all levels of scrambling [11]. This important result is clearly consistent with our data, as it indicates that greater global pooling occurs in V4 than in V1, and that V4 pooling is configural rather than random (random pooling would predict equal activation of V4 by large image components and by a highly scrambled image). Surface recordings from the brains of human subjects prior to epilepsy surgery [12] provide strong convergent support for this conclusion. Evoked responses (N180) recorded from the ventral surface of the brain posterior to face-selective sites (but anterior to V1) showed significant selectivity for concentric and radial gratings as opposed to sinusoidal gratings, consistent with the data of Gallant *et al.* [4,5] and the present study. Although their electrophysiological methods did not allow precise localization relative to anatomical boundaries, the authors tentatively identified the area as human V4 [12]. The fMRI results of the present study thus provide a direct link between these surface recordings and human V4 as defined by retinotopic mapping.

One recent physiological study has suggested that critical tuning dimensions for many macaque V4 neurons may be convex curvature and angularity [13]. Our fMRI results are consistent with this but cannot discriminate between these more general stimulus properties as opposed to concentric and radial structure *per se*. Another recent study [14] has reported that enhanced sensitivity to curved and angular stimuli may occur as early as V2. Therefore, we analyzed V2 data from our subjects and found a trend towards greater sensitivity to concentric and radial structure compared with parallel, but this trend was not statistically significant.

While the main focus of this study was on the role of V4 in pooling orientation information, we also predicted that brain regions involved in face perception might show a bias for concentric patterns because of the importance of quasi-circular structure in defining head shape [15]. In the FFA, concentric gratings were by far the strongest geometric stimuli, producing significantly more activation than

Table 1

Statistical comparisons (pairwise *t*-tests) of activation by the three geometric pattern types.

Area	Concentric versus radial	Concentric versus parallel	Radial versus parallel
V1	$t_4 = 1.37$*	$t_4 = 1.03$*	$t_4 = -0.17$*
V4	$t_4 = 0.13$*	$t_4 = 3.27$, $p < 0.05$	$t_4 = 3.36$, $p < 0.05$
FFA	$t_4 = 3.53$, $p < 0.05$	$t_4 = 5.70$, $p < 0.005$	$t_4 = 1.79$*

*Not statistically significant.

either the radial or parallel patterns (Figure 4, Table 1). Indeed, concentric gratings produced roughly half as much activation as faces in the FFA, supporting our suggestion that analysis of concentric structure may be an important aspect of face perception [15]. However, we speculate that both concentric and radial structures extracted in V4 may contribute to the analysis of a much wider range of objects. Thus, future work on both the physiology and psychophysics of intermediate level form vision should profit from the use of concentric, radial and other configural stimuli, in preference to simple bars or conventional sinusoidal gratings.

Supplementary material

Supplementary material including additional methodological detail and a figure showing the spatial frequency composition of the face and object stimuli is available at http://current-biology.com/supmat/supmatin.htm.

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